The status, ecology and relationships of *Meziella* (Haloragaceae)

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Abstract

Orchard, A.E. and Keighery, G.J. The status, ecology and relationships of *Meziella* (Haloragaceae). Nuytsia 9(1): 111-117 (1993). The monotypic genus *Meziella* has until now been known only from its very fragmentary and immature type. Because of this its status as a genus and relationships have been unclear, and its description has been incomplete. Recent rediscovery of the species has allowed a full description to be prepared for the first time. It is now confirmed that *Meziella* is a distinct genus, intermediate in many respects between *Haloragis* and *Myriophyllum*. Its somewhat bizarre features are described, its ecology discussed, and a revised key to the Australian genera of the family is provided.

Introduction

Nees (1844) described a new species, *Gonocarpus trifidus,* from a Preiss collection from the shores of a lake near Albany in Western Australia. The plant was a small creeping herb, rooting at the nodes, with trifid leaves and young flowers. The main collection was deposited in the Nees collection at LE, but a small fragment subsequently found its way to MEL.

Two years later, Walpers (1846) transferred the species to *Haloragis*, probably for no better reason than that it was considered that the two genera were synonymous. There is no indication that he re-examined the species, and even if he had, it is unlikely that he could have made much of it with only immature flowers to work with.

The only complete revision of the family Haloragaceae to species level since Walper's treatment is that of Schindler (1905). He recognised two subfamilies, Halorrhagoideae and Gunneroideae, the second of which is now generally considered to constitute a distinct family, Gunneraceae. Schindler divided subfamily Halorrhagoideae into two tribes, Halorrhageae and Myriophylleae, distinguished by the characters of the endocarp. In tribe Halorrhageae the 1-4-locular ovary develops into a fruit in which the woody or crustaceous endocarp constitutes a single structure, and the 1-4 seeds in each fruit are shed as a unit within the dry nut. In tribe Myriophylleae, containing only the genus *Myriophyllum*, the woody endocarp forms separately around each locule, and at maturity the fruit separates into two or four 1-seeded nutlets.

Schindler re-examined the single collection of "*Haloragis trifida*", and decided, despite its deficiencies, to segregate it as a distinct genus from *Haloragis* (which also included *Gonocarpus*).

a principal distinguishing character he used the fact that in *Meziella* (as he called it), the sepals were much longer than the ovary, whereas in *Haloragis sensu lato* they were much shorter. He also drew attention to the fact that *Meziella* had only a single whorl of 4 stamens, whereas most species of *Haloragis* had a double whorl totalling 6 or 8 (the only exception known to him being *Haloragis* (= *Gonocarpus*) *nodulosa*.

In a series of papers, Orchard (1975, 1976, 1977, 1979, 1980, 1981, 1986a, 1986b, 1990a, 1990b), revised the generic and specific taxonomy of the South American, Pacific and Australian members of the family. In general Orchard adopted the generic circumscription of Schindler, with two major differences. *Gonocarpus* was re-instated as a genus distinct from *Haloragis,* and a new genus *Haloragodendron* was created. In both cases the critical distinguishing characters were to be found in the development of the ovary into the fruit. The flowers of *Gonocarpus, Haloragis* and *Haloragodendron* all begin with four ovules in an ovary with essentially 4 locules (sometimes reduced to 2 or 3 ovules and locules). In *Gonocarpus* the septa are insubstantial and incomplete, and are crushed by the single ovule which develops into a seed. The ovary wall becomes crustaceous in fruit, but hardly woody. In *Haloragis* all 4 ovules can potentially develop into seeds, and the septa and endocarp become woody, forming a single, indehiscent, dry, 4-seeded nut which is shed as a single unit. *Haloragodendron* has a fruit development somewhat intermediate between *Gonocarpus* and *Haloragis.* In the flower the ovary has substantial and complete septa between the 4 locules (resembling *Haloragis*), but only a single seed is formed in each fruit, crushing the septa to one side (as in *Gonocarpus*). However, the endocarp becomes very woody, and the fruit increases in size considerably after anthesis (both characteristic of *Haloragis*, but not of *Gonocarpus*). Other characters support this generic disposition, but the developmental characters of the ovary/fruit were found to be the most diagnostic.

Orchard considered the status of *Meziella* in two papers (1975, 1990b), but because of the paucity and poor quality of the material available was unable to decide on the exact generic status of the species, and opted to maintain the *status quo* until more material became available. Attention was drawn to the superficial similarity of the habit and vegetative morphology of *Meziella* to some bog-dwelling small species of *Myriophyllum*. For example, *Myriophyllum limnophilum* has a very close resemblance to *Meziella* in habit and leaf shape, and is also found in boggy ground in the south-west of Western Australia. However, without fruits it was impossible to decide whether *Meziella* was in fact a distinct genus, or only a species of *Haloragis* or *Myriophyllum*. In the last 10 years several searches have been made in an attempt to re-discover *Meziella*, but in the absence of details of its original collection site, all failed, and it was feared that the species (and genus) had become extinct.

Recently one of us (G.J.K.) discovered a population of a strange bog-dwelling plant at Chester Forest Block (34° 11' S, 115° 19' E), approximately 30 km east of Augusta, and about 200 km west of Preiss' original collection from near Albany, but still in the Warren Botanical Subdistrict. Examination has confirmed it to be *Meziella*. The new discovery bore copious flowers and fruits, and these have finally allowed the question of the status of the genus to be resolved. In addition, the ecology of the species can now be described.

Chester Block occupies the only remnant of the Nillup Plain remaining uncleared. This area is a gently sloping pediment of the Blackwood Plateau, and is normally saturated or slightly submerged during winter and spring. *Meziella* occurs on slightly submerged flats, on grey sandy clays over clay. It is found in very shallow (c. 5 cm deep) pools or prostrate on saturated soils in slight depressions. Vegetation is a low heath of *Pericalymma crassipes* over mixed sedges (chiefly *Leptocarpus* and *Restio* species). Scattered through this community are emergent trees of *Melaleuca rhaphiophylla* and tall shrubs of *Adenanthos detmoldii*.

Meziella can over-summer in protected sites as a small rootstock with short dense leafy stems with linear leaves. However, many plants in drier more exposed sites die during the summer. Regrowth and germination occurs as the winter rains flood the small depressions and continues until the area begins to dry in October and November.

Flowering commences during November at Chester Block and continues until January. Mature fruits are present from January to February. Flowering ceases in January and the plants die or over-summer as vegetative shoots until the next winter. Dispersal of the fruit has not yet been observed.

The status of *Meziella*

Meziella is a fairly bizarre plant at first sight, but perhaps no more so than some of the more unusual species of *Myriophyllum,* such as *M. callitrichoides, M. decussatum* or *M. coronatum.* In habit it resembles several of the small bog-dwelling semi-aquatic species of *Myriophyllum.* The flowers are bisexual, with the 4-merous plan common in Haloragaceae, but have disproportionately long and narrow sepals almost equalling the petals, unlike any other species in the family. In fruit these sepals become stiffly erect or semi-spreading, forming a corona of soft spines at the summit of the fruit. At the same time further soft spine-like processes are developed in the lower half of the fruit, with groups of 6-7 "spines" below each sepal. These lower spines are present in the flower, but are very reduced, and expand rapidly once the petals and stamens are shed. They were not observed by any previous author.

The stamens of *Meziella* are also somewhat unusual. Only a single whorl of 4 is present, unlike the double whorl normal in the family. This reduction in number occurs occasionally in other genera, e.g. in *Gonocarpus nodulosus, Myriophyllum integrifolium, M. limnophilum, M. callitrichoides* subsp. *callitrichoides* and *M. mattogrossense,* but is not common. In addition, the anthers in *Meziella* are distinctly apiculate. This is an unusual feature in the family, found in most species of *Glischrocaryon,* all species of *Haloragodendron,* and rarely in *Myriophyllum* (e.g. *M. coronatum, M. muricatum, M. mattogrossense*).

As in many other Haloragaceae, while the flowers of *Meziella* are morphologically bisexual, they are often functionally unisexual. In the inflorescence there is a gradation from flowers at the top of the spike which are functionally male by virtue of their protandry, and which through truncation of the growing season will probably never develop their female parts, to those in the central region of the spike which, having shed their pollen develop their stigmas, become pollinated themselves and develop rapidly to fruit, and those towards the base of the spike in which the anthers, although present, do not split open to release pollen and are thus functionally female. A similar gradation is not unusual in many species of *Myriophyllum,* and in some species of *Haloragis* and *Gonocarpus.*

The ovary/fruit development provides the final evidence that *Meziella* deserves its separate generic status. The ovary is 4-locular with well-defined septa, and a single pendulous ovule in each locule (i.e. identical with *Haloragis* and *Haloragodendron*). Each of these ovules develops, potentially, to form a seed. In the process the endocarp around each locule becomes woody, but unlike *Haloragis,* where a single 4-locular woody mass is formed, in *Meziella* 4 separate woody 1-seeded pyrenes develop. This is similar to the situation in *Myriophyllum,* but there the exocarp splits to allow the mericarps to separate for dispersal. This does not happen in *Meziella.* Here the fruit remains indehiscent, and the four pyrenes or mericarps are shed as a unit, bound together by the spiny exocarp.

The above combination of characters is sufficient to confirm the status of *Meziella* as a distinct genus. Its relationships seem to be with *Myriophyllum*, with which it shares its sub-aquatic habit, dissected leaves, and fruits in which the endocarp becomes woody around each individual locule rather than around the fruit as a whole. However it differs from *Myriophyllum* in that the fruit does not separate into mericarps at maturity. The subulate sepals, equalling the petals in length, and persisting as spines on the fruit, serve to set the taxon apart from all others in the family.

Schindler's higher level classification needs modification with the discovery of the developmental structure of the fruit in *Meziella*. His tribe Myriophylleae was established on the basis that *Myriophyllum* differed from all other genera in having a fruit which split into mericarps at maturity, whereas the fruits of the genera comprising tribe Halorrhageae were completely indehiscent. *Meziella* straddles this divide. However it can be accommodated if tribe Myriophylleae is redefined as having a fruit made up of 1-seeded pyrenes, while tribe Halorrhageae has a fruit in which all carpels are fused into a single unit, which may contain as few as 1 seed, or as many as 4, but is never divided into pyrenes. This modified classification is reflected in the key to genera below.

Key to the genera of Haloragaceae

1. Fruit an indehiscent 1-4-seeded nut not subdivided into 1-seeded pyrenes ..... Tribe Halorrhageae
   2. All flowers with petals
      3. Petals hooded; anthers non-apiculate; inflorescence indeterminate
         4. Fruits (2-3)4-locular, pericarp woody with solid septa; flowers in (1)3-7-flowered dichasia in the axils of alternate bracts ..... *Haloragis*
         4. Fruits 1-locular, pericarp crustaceous with no septa (crushed by single seed); flowers solitary (very rarely 1-3) in the axils of opposite or alternate bracts ..... *Gonocarpus*
      3. Petals navicular; anthers usually apiculate; inflorescence determinate
         5. Leaves serrate; inflorescence narrow, spike-like; shrubs or small trees with 1-few woody stems/trunks ..... *Haloragodendron*
         5. Leaves entire; inflorescence broad, pseudo-umbelliform; subshrubs with numerous annual stems arising from a perennial rootstock ..... *Glischrocaryon*
   2. At least female flowers lacking petals (rudimentary petals in *Proserpinaca*)
      6. Fruit 1-locular; flowers predominantly unisexual, in dichasia of up to about 11 flowers per axil, the terminal one in each dichasium usually male, the others female or rarely bisexual; anthers linear-oblong ..... *Laurembergia*
      6. Fruit 3-locular; flowers bisexual, solitary or in dichasia of up to 3 flowers per axil; anthers ellipsoid ..... *Proserpinaca*
1. Fruit made up of 1-seeded pyrenes ..... Tribe Myriophylleae
   7. Fruit splitting at maturity into mericarps; sepals less than half length of petals (frequently absent), flat, lanceolate to ovate; flowers frequently unisexual ..... *Myriophyllum*
   7. Fruit not splitting at maturity into mericarps; sepals almost equalling petals in length, subulate, developing into soft spines; flowers bisexual ..... *Meziella*

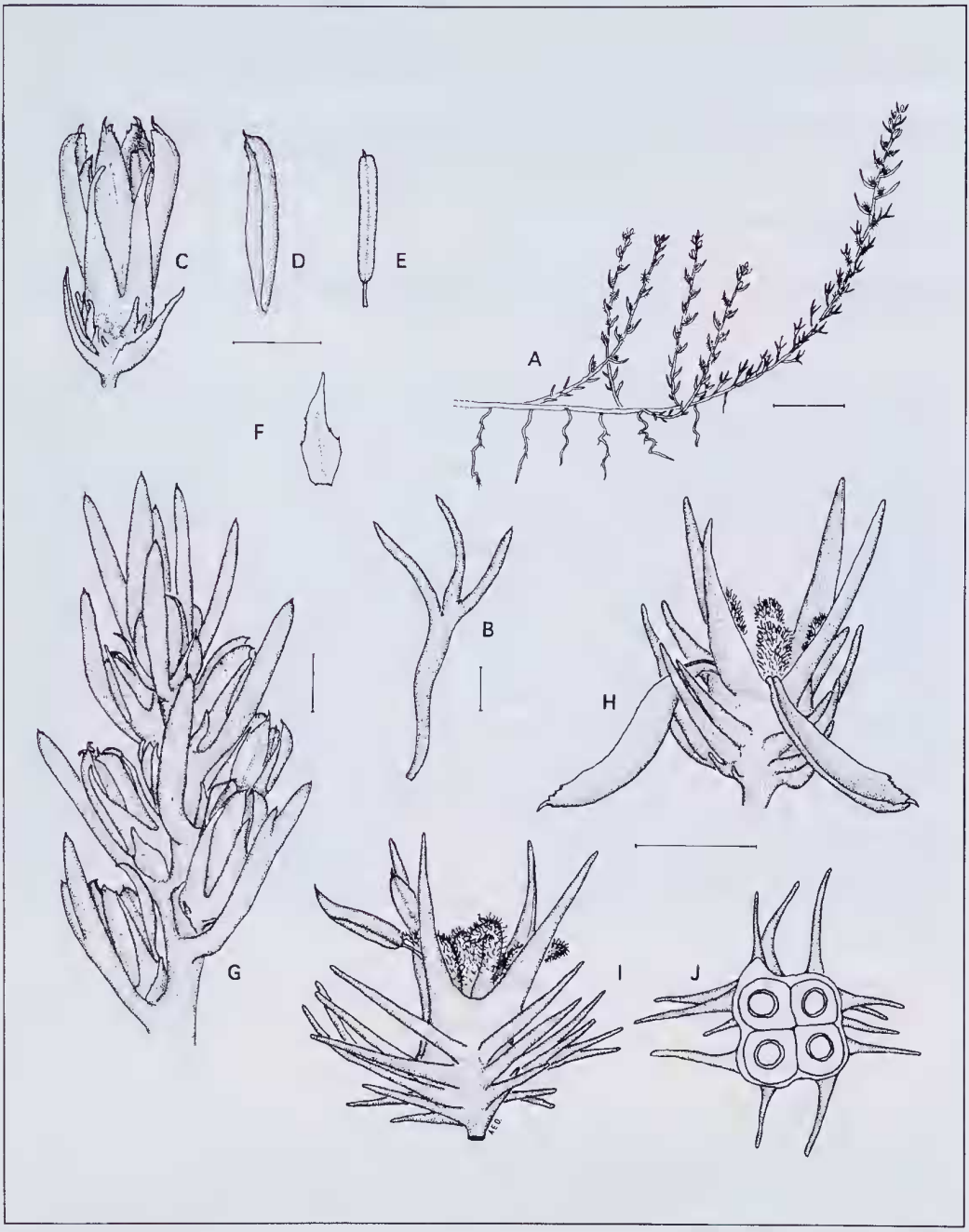

Figure 1. *Meziella trifida*. A - habit. B - trifid leaf from the mid-stem region. C - flower subtended by two bracteoles. D - petal. E - stamen. F - bracteole. G - tip of inflorescence showing buds, and flowers at anthesis. H - old flower/young fruit. I - mature fruit. J - transverse section of fruit showing the four pyrenes within a single pericarp. Scales represent 1 cm (A) or 1 mm (B-J). All illustrations are from *Keighery* 12789.

Description of *Meziella trifida*

Meziella trifida (Nees) Schindler, Pflanzenr. 23: 61 (1905) (Figure 1)

Gonocarpus ['Goniocarpus'] *trifidus* Nees in Lehm., Pl. Preiss. 1: 159 (1844)

Typus: "In turfosis humidis ad lacum haud procul ab oppidulo Albany (Plantagenet) m. Octobri 1840. Herb. Preiss. No. 2401". Holo: LE; iso: MEL

Haloragis trifida (Nees) Walp., Rep. 5: 672 (1846)

Illustrations: Schindler, Pflanzenr. 23: 61, fig. 18 (1905); Blackall & Grieve, W. Austral. Wildfls 3: 463, 472 (1965); Orchard, Fl. Austral. 18: 86, fig. 29 A-F.

Decumbent, glabrous, annual or perennial *semi-aquatic herb*, reddish in most parts; main *stems* prostrate, rooting at the nodes, freely branched; lateral stems ascending, apparently all becoming fertile. *Leaves* alternate, subfleshy, the lowermost on each stem entire, linear, 3.5-5.0 mm long, 0.4 mm wide, sessile, tip acute; middle and upper leaves on each stem becoming trifid with 2 linear lobes at or above the middle and ± equalling central lobe in length; each lobe tipped with a hydathode, and tiny hydathodes sometimes also present in the axils of the lobes. *Inflorescence* an indeterminate spike of flowers borne singly in the axils of slightly reduced upper leaves (bracts) on each lateral stem. *Bracts* trifid in the lower part, becoming entire above, leaflike. Each flower subtended by a pair of lanceolate or narrowly deltoid bracteoles, which are red, acute, entire, 1.0 mm long, 0.3 mm wide. *Flowers* 4-merous, bisexual, sessile. *Sepals* 4, red, subulate, 1.7 mm long, 0.3-0.35 mm wide, entire, smooth, erect. *Petals* 4, red, narrowly hooded, 1.7-1.8 mm long, 0.2 mm wide (keel to margin), with a distinct apiculum; shed almost immediately after anthesis. *Stamens* 4, antisepalous; *filaments* deep red, lengthening to 0.4-0.5 mm; *anthers* yellow to reddish, narrowly oblong, 1.2 mm long, 0.25 mm wide, distinctly apiculate, sometimes indehiscent in lower flowers. *Styles* 4, reddish, clavate; *stigma* papillate. *Ovary* small, c. 0.5 mm diameter, ± globular, with clusters of short subulate processes below the sepals; 4-locular; expanding rapidly in fruit. *Fruit* red, indehiscent, of 4 woody 1-seeded pyrenes contained within a dry exocarp. Sepals persistent, increasing in size and thickness to form a terminal corona; clusters of 6-7 soft spreading spines to 1.3 mm long develop on the lower half of the torus beneath each sepal, upper half of torus smooth. Fruit (including spines) c. 2.7 mm long, 2.7 mm in diameter.

Specimens of the new collection (*G. Keighery* 12789) have been lodged at PERTH and HO.

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